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THE SPATIAL DISTRIBUTION OF ENDEMIC AND INTRODUCED FLOWER-BREEDING SPECIES OF *DROSOPHILA* (DIPTERA: DROSOPHILIDAE) DURING THEIR EARLY HISTORY OF ENCOUNTER ON THE ISLAND OF HAWAII

William T. Starmer[1] and Jane M. Bowles[2]
[1]Department of Biology, Syracuse University, Syracuse, New York 13244;
[2]Department of Plant Sciences, University of Western Ontario, London, Ontario N6A 5B7

Abstract.—The spatial distribution of two flower-breeding drosophilids (an endemic, *Scaptomyza caliginosa* Hardy and an exotic, *Drosophila floricola* Sturtevant) is reported for morning and evening censuses of four sites at one locality on the island of Hawaii. The increase in the relative frequency of the introduced species over the last 10 years appears to be due to the increase in the number of adult *D. floricola* and not a reduction in number of endemic adult *S. caliginosa.* The analysis indicates that the two species are sympatric and adults occupy the same individual blossoms of morning glory. Afternoon and evening aggregation behavior of adult *S. caliginosa* may explain some variation in the joint distribution of the two species. Although there is some evidence for the adults using different blossoms, there is considerable overlap of adults of the two species in the same blossoms and it is concluded that the potential for larval-larval competition between the two species is high.

Key Words.—Insecta, Diptera, *Scaptomyza* (*Exalloscaptomyza*) *caliginosa, Drosophila* (*Phloridosa*) *floricola,* morning glory, flower breeders, Hawaiian drosophilids, spatial distribution, coexistence

For 12 years we have been monitoring the population densities of two drosophilid species that breed in blossoms of the morning glory, *Ipomoea acuminata* (Vahl) Roemer & Schultes, on the island of Hawaii in the Hawaiian Archipelago. One species, *Scaptomyza* (*Exalloscaptomyza*) *caliginosa* Hardy, is endemic to Hawaii and uses only morning glory blossoms as a larval and adult feeding substrate (Hardy 1965, 1966; Ibara 1976). The other species, *Drosophila* (*Phloridosa*) *floricola* Sturtevant, was introduced to Hawaii about 15–20 years ago and also uses flowers, including morning glories, as breeding sites. Montague & Kaneshiro (1982) reported the percentage of adults to be 96% *S. caliginosa* and 4% *D. floricola* in morning glory flowers growing in Kipuka Puaulu (Bird Park) Hawaii Volcanoes National Park on Hawaii Island during September and November 1980. Since then we have several estimates of the numbers of both species in the same and neighboring sites. These counts reveal a striking change in the relative numbers of the two species and prompted us to determine the distribution of the two species in the same area.

This paper reports counts of both species made in Bird Park and neighboring areas since 1980 and analyzes the spatial distribution of the adults occupying individual flowers during October 1991. This analysis provides a basis for studying the competitive interactions of two species in early stages of sympatry (Montague & Kaneshiro 1982). The species evolved their flower breeding habit independently and have different life-history characteristics. Montague & Kaneshiro (1982) emphasized differences in reproductive potential and in the larval stage as important facets of the ultimate fate of the two species in this habitat. The introduced species has a greater reproductive potential (i.e., 13.5 ovarioles per female for *D. floricola* and 1.05 ovarioles per female for *S. caliginosa*). The endemic female, however, either deposits a single large egg, that hatches soon after being laid, or a precocious larva in a flower. The introduced female lays several eggs that must mature before hatching. These differences might be important if adults and larvae of the two species share the same resources to an extent. There are several levels of resource sharing that can be considered. These include 1) sharing the same sites where flowers grow, 2) sharing the same individual blossoms of the morning glory, and 3) using the resources available in a shared blossom in the same way. The first two considerations are the concerns of this report. We focus on adult distributions because this could separate the two species spatially and thus preclude larval competition.

Material and Methods

The spatial distribution of adult *S. caliginosa* and *D. floricola* was determined by counting the number of each species in individual morning glory blossoms over a two day period (30–31 Oct 1991). Sites in Kipuka Puaulu (Bird Park) and alongside the road between Bird Park and Kipuka Ki were censused in the morning (8:00–10:00 h = AM) and afternoon (15:00–17:00 h = PM). Adult flies present in 100 blossoms were counted at each site and each blossom was mapped by systematically walking through the area and plotting their Cartesian coordinates. The number of adults in most of the blossoms in a contiguous area were counted. In some cases when flies were inadvertently frightened away, the blossom was skipped. Flies were counted either directly in the blossom or after being aspirated into a glass vial using a magnifying glass (2×). All flies that were aspirated were released after counting. Some adults were trapped by placing a plastic bag over the blossom and returning it to the laboratory. In these cases the site was being censused for the second and last time.

Two sites (A & B) within Bird Park and two sites (A & B) along the road between Bird Park and Kipuka Ki were censused. The area surveyed at each site varied as a function of flower density because the number of blossoms mapped was held constant at 100 blossoms. The approximate area mapped for each site was 227, 177, 60 and 62 m^2 for Bird Park-A, Bird Park-B, Road-A and Road-B respectively. The Bird Park sites were located along the main trail in open fields and were separated by intervening forest with no morning glories present. Site A was north of the entrance to the park and site B was east of the entrance. The road sites were between Bird Park and Kipuka Ki. Although morning glory vines were continuous along the road in this area, the two sites were on opposite sides of the road at a distance of 1.1 km (site A) and 1 km (site B) from the gate at Bird Park. Two sites (Road-A, Bird Park-A) were censused on the first morning (30 Oct 1991) and again on the afternoon of the next day (31 Oct 1991). Two sites (Road-B, Bird Park-B) censused on the first afternoon were censused again on the following morning. This procedure was followed because disturbance in the morning is more likely to affect the afternoon distribution, while an afternoon census is less likely to affect the census on the following morning when most flies move to and occupy newly opened blossoms.

Table 1. Percentage of adults of the endemic species *Scaptomyza caliginosa* relative to the introduced species *Drosophila floricola* present in Bird Park and neighboring areas.

Date of census	Bird Park		Road		Collector
1976	100.0				Ibara (1976)
Aug 1978	100.0				J. R. Montague & W. T. Starmer[a]
Sep–Nov 1980	96.3				Montague & Kaneshiro (1982)
3–8 Dec 1987	97.9				W. T. Starmer, D. Droney, & J. Bowles[a]
2 Jun 1989			~50		K. Kaneshiro[a]
Jan 1990			~50		M. Kambysellis[a]
	Site A	Site B	Site A	Site B	
16 Aug 1990	57.4	60.5	7.5	3.3	M. Tlusty[a]
27 Aug 1990	27.5	46.3	49.4		D. Droney[a]
30–31 Oct 1991	83.9	35.7	87.0	52.7	This study

[a] Personal communications.

The joint occurrence of the two species was analyzed with correlations for the number of adults of each species in a flower and by calculating the G-statistic on 2-way tables of presence or absence of the two species. In addition 2-way tables with three levels (absent, 1 adult and >1 adult per flower) for each species were analyzed for each census.

A plot of the autocorrelation coefficients as a function of distance is termed an "I correlogram" when the correlations calculated are product-moment correlations (Sokal & Oden 1978a, b). I correlograms of the number of adults per flower were calculated for *S. caliginosa* versus *S. caliginosa, D. floricola* versus *D. floricola* and for *S. caliginosa* versus *D. floricola.* The correlations were determined for each census locality (Bird Park-A, Bird Park-B, Road-A, Road-B) at each time of day (AM, PM). A step size of 2 m was chosen and spatial correlations (i.e., product-moment correlations for number of adults in a flower) for all pairs of flowers at distances of 0–2, 2–4, 4–6 . . . 28–30 m were calculated. These correlations were based on an average sample size of 555 pairs of flowers for any one distance. At this level, correlations between −0.12 and +0.12 would be considered nonsignificant at $\alpha = 0.01$.

Results

The numbers of *D. floricola* were low until 1988 when they increased (Table 1). Our recent records (Table 2) indicate that the number of *S. caliginosa* per blossom has remained about the same as that observed in 1980 (0.77, 2.56 and 3.12 adults per blossom for covered, sunlit and shrub blossoms respectively, table 1 of Montague & Kaneshiro 1982) and on 16 Aug 1990 (2.77 adults per blossom). Only the Bird Park-B site had lower numbers in the present survey.

Although morning glory blossoms are considered to remain open for only one day, some blossoms will stay open for two days at lower temperatures. We recorded the number of 1st and 2nd day (i.e., new and old) blossoms during each census. The average ratio was 3 new : 1 old for all sites. An analysis of variance on the average number of adults in new versus old blossoms for each census (site, time, species) did not reveal a significant effect of flower age on the average number of

Table 2. Number of adults per blossom, correlation between number of adults of the two species and the percentage of *Scaptomyza caliginosa* for each census.

Site		*S. caliginosa*		*D. floricola*			Correlation[a]	
							Empty blossoms	
		Average adults/ flower	Standard deviation	Average adults/ flower	Standard deviation	Percentage *S. caliginosa*	Included	Excluded
Bird Park A	(AM)	2.19	4.35	0.34	0.77	86.51	0.104	0.044
	(PM)	1.93	4.04	0.45	0.94	81.09	−0.101	−0.243*
Bird Park B	(AM)	0.28	0.51	0.48	0.94	36.84	−0.093	−0.574***
	(PM)	0.37	0.65	0.69	1.17	33.65	−0.047	−0.356**
Road A	(AM)	1.67	2.03	0.47	0.76	78.04	−0.023	−0.109
	(PM)	4.06	13.48	0.39	0.98	91.24	−0.023	−0.098
Road B	(AM)	1.01	1.26	0.54	0.93	65.16	−0.074	−0.253*
	(PM)	0.67	0.87	0.97	2.34	40.85	−0.045	−0.256*

[a] The correlations were estimated from the number of adults of each species present in each blossom. The included column includes blossoms that had no flies present, whereas the excluded column does not include empty blossoms.

*, **, *** Represent significance at 0.05, 0.01 and 0.001, respectively.

adults per blossom ($F = 0.91$; df = 6, 1; $P > 0.10$) or significant interactions between age of flower with the other factors (site, time or species). We considered all flowers in each census to be equivalent in the following analyses.

The Bird Park sites show different frequencies of *D. floricola* at each site but morning versus afternoon percentage for each site remained constant. The Road site percentages differed from site to site and for the two sampling periods. Most variance to mean ratios are greater than one, indicating that the flies have aggregated rather than random or evenly dispersed distributions. This is especially apparent for *S. caliginosa* at Road site A in the evening where six flowers had greater than 26 flies per flower and accounted for 75% of the adults in the 100 flowers sampled (Table 3). The correlations for number of adults of each species in a flower are significantly negative (if empty blossoms are excluded) for 5 of the 8 censuses (Table 2). This indicates a general trend for the adults of the two species to occupy different flowers. If the average number of flies per blossom for each species is used as observations (Table 2) to estimate site to site correlations in the density of each species the estimate is also negative but non-significant ($r = -0.58$, df = 6, $P > 0.10$).

In six of the eight analyses in Table 4 the two species are independently distributed. However, during the morning at both Road sites the distribution of one species is dependent on the distribution of the other. In these cases the observed number of flowers where 1) both species are present and 2) both are absent (i.e., empty) are lower than expected. A similar analysis where three categories (absent, 1 adult and >1 adult per blossom) for each species were considered revealed the same pattern. That is, the only significant G-statistics were for the two Road sites in the morning and these showed lower than expected numbers for flowers containing both species and flowers that were empty.

The I correlograms for *S. caliginosa* versus *S. caliginosa, D. floricola* versus *D. floricola* and for *S. caliginosa* versus *D. floricola* are shown in Figs. 1, 2 and 3 respectively. The correlograms show that there is little spatial structure in the populations of each species and between the two species. Another spatial auto-

Table 3. Number of adult flies per blossom of *Scaptomyza caliginosa* (Sc) and *Drosophila floricola* (Df) at the four sites.

	Bird Park								Road							
	A				B				A				B			
	AM		PM		AM		PM		AM		PM		AM		PM	
Adults per blossom	Sc	Df	Sc	Df	Sc	Df	Sc	Df	Sc	Df	Sc	Df	Sc	Df	Sc	Df
0	33	76	47	75	75	71	71	61	27	67	49	79	42	67	53	68
1	29	19	21	13	22	18	22	23	35	21	23	13	34	18	32	14
2	15	2	16	6	3	6	6	9	21	10	13	4	12	11	11	7
3	9	2	2	5		3	1	3	6	2	4		9	3	3	2
4	3		2			1		3	1		1	2	2		1	4
5	3	1	2	1		1			4		1	2		1		1
6	4		2						2							1
7			3					1			2					
8	1								1				1			
9			1						2							1
10									1							
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Total flies counted	219	34	193	45	28	48	37	69	167	47	406	39	101	54	67	97

correlation analysis was conducted with the empty flowers at each site removed from the data set. This analysis resulted in different estimates of the correlations but did not reveal significant spatial structure for either species or the two species considered together.

Discussion

Variation in the number of adults of each species present at each site can be explained in several ways. The two sites in Bird Park (Table 2) were similar in many respects except that the B-site was contiguous with an area that had been

Table 4. Two-way tables for the distribution of *Scaptomyza caliginosa* (Sc) and *Drosophila floricola* (Df) in 100 blossoms for each census. The *G* statistic has 1 degree of freedom.

	Morning				Evening			
		Sc				Sc		
	Df	+	−	*G*	Df	+	−	*G*
Bird Park A	+	13	11	2.28	+	11	14	1.08
	−	54	22		−	42	33	
Bird Park B	+	6	23	0.42	+	8	31	2.30
	−	19	52		−	21	40	
Road A	+	19	14	5.73*	+	8	13	1.78
	−	54	13		−	43	36	
Road B	+	14	19	4.88*	+	12	20	1.72
	−	44	23		−	35	33	

* Significant at $\alpha < 0.05$.

defoliated with herbicide (applied after the 27 Aug 1990 census). Some of the variance for the number and relative proportions of the adults of the two species at the road sites may be due to the vertical distribution of the flowers at the two sites. The flowers along the side of the road at the A-site were below two meters and accessible, while the vines at the B-site exceeded 2 to 3 meters making the highest flowers in the vicinity inaccessible. Because adults of *S. caliginosa* tend to accumulate in higher blossoms in the afternoon and evening, it was not possible to count those flowers with large numbers of flies higher in the canopy. Thus the relative increase in *D. floricola* adults during the afternoon at the B-site (Table 2) is probably due to the movement of *S. caliginosa* adults into the higher blossoms. This may also be an important consideration in interpreting the counts made beside the road on 16 Aug 1990 (Table 1) since those blossoms were collected in the evening after the movement of *S. caliginosa* into focal blossoms.

Most of the variation in percentage of *D. floricola* is due to changes in numbers of *S. caliginosa.* This could be due to movement of *S. caliginosa* as mentioned for the Road-site B as well as between site differences in the number of *S. caliginosa* present. This can be seen in the mean to variance ratios across sites (observations from Table 2) for *S. caliginosa* (1.52:1.56) as compared to (0.54:0.04) for *D. floricola.* Although the average number of *S. caliginosa* per blossom has not changed in the Bird Park area over years, the variation from site to site is considerable.

Although the correlograms (Figs. 1, 2 and 3) show little spatial structure, there does appear to be a trend in the *S. caliginosa* population for positive correlations at the closer distances and negative correlations at the further distances (Fig. 1). This is possibly due to the aggregation behavior of *S. caliginosa.* This behavior would result in patches of blossoms with higher than average numbers of adults in the flowers close to the focal flowers as *S. caliginosa* adults aggregate in afternoon and evening and would have the same effect as they move to newly opened blossoms in the morning. That is, many newly opened blossoms close to the focal aggregate blossoms would have higher numbers of adults due to their proximity to that blossom.

Fisher (1991) showed that when both species are kept together in laboratory

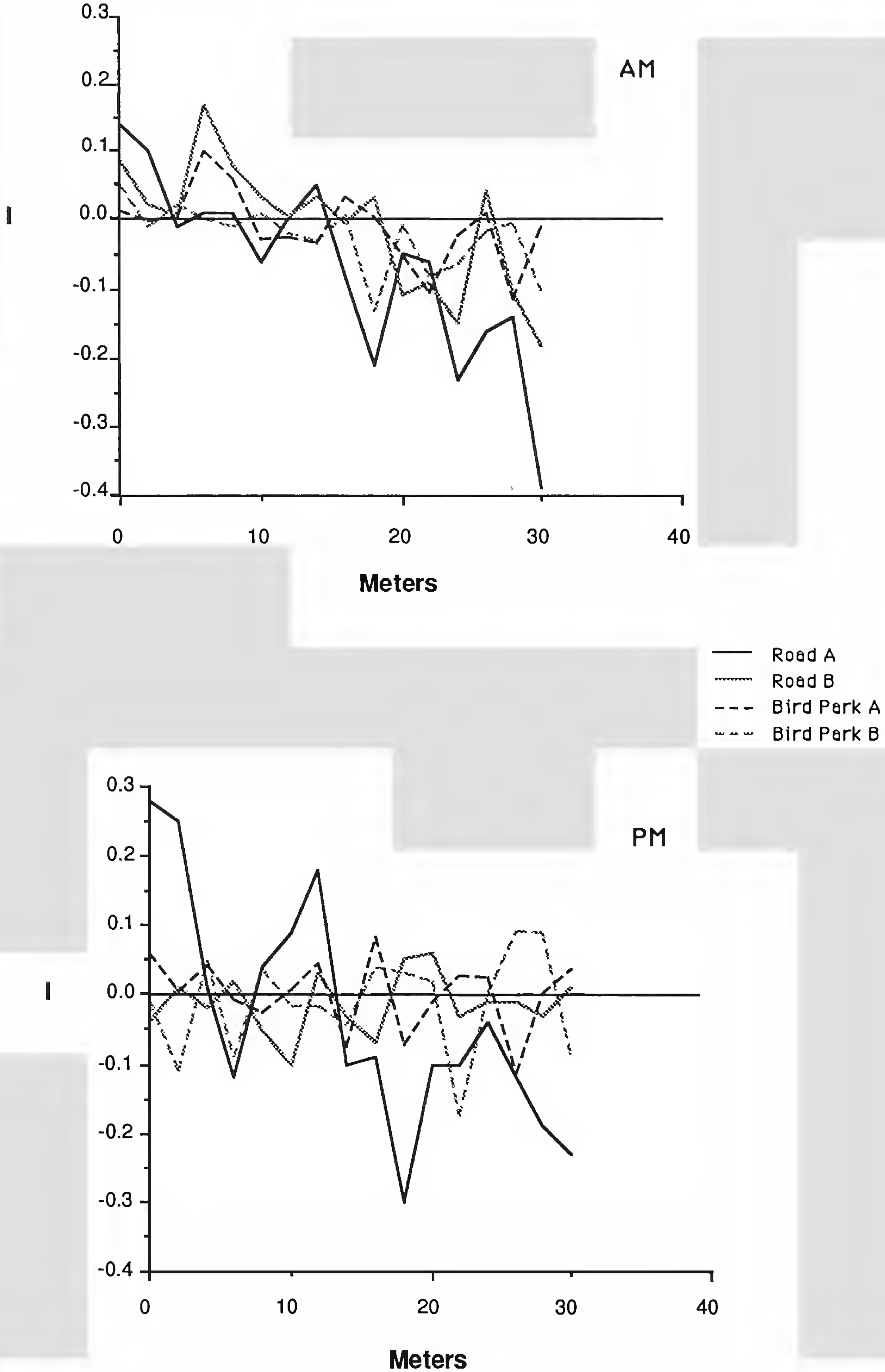

Figure 1. Correlogram for the number of *S. caliginosa* versus *S. caliginosa* adults per blossom as a function of distance (meters) between blossoms. The four lines represent the four sites. The upper and lower figures are for morning and evening censuses, respectively.

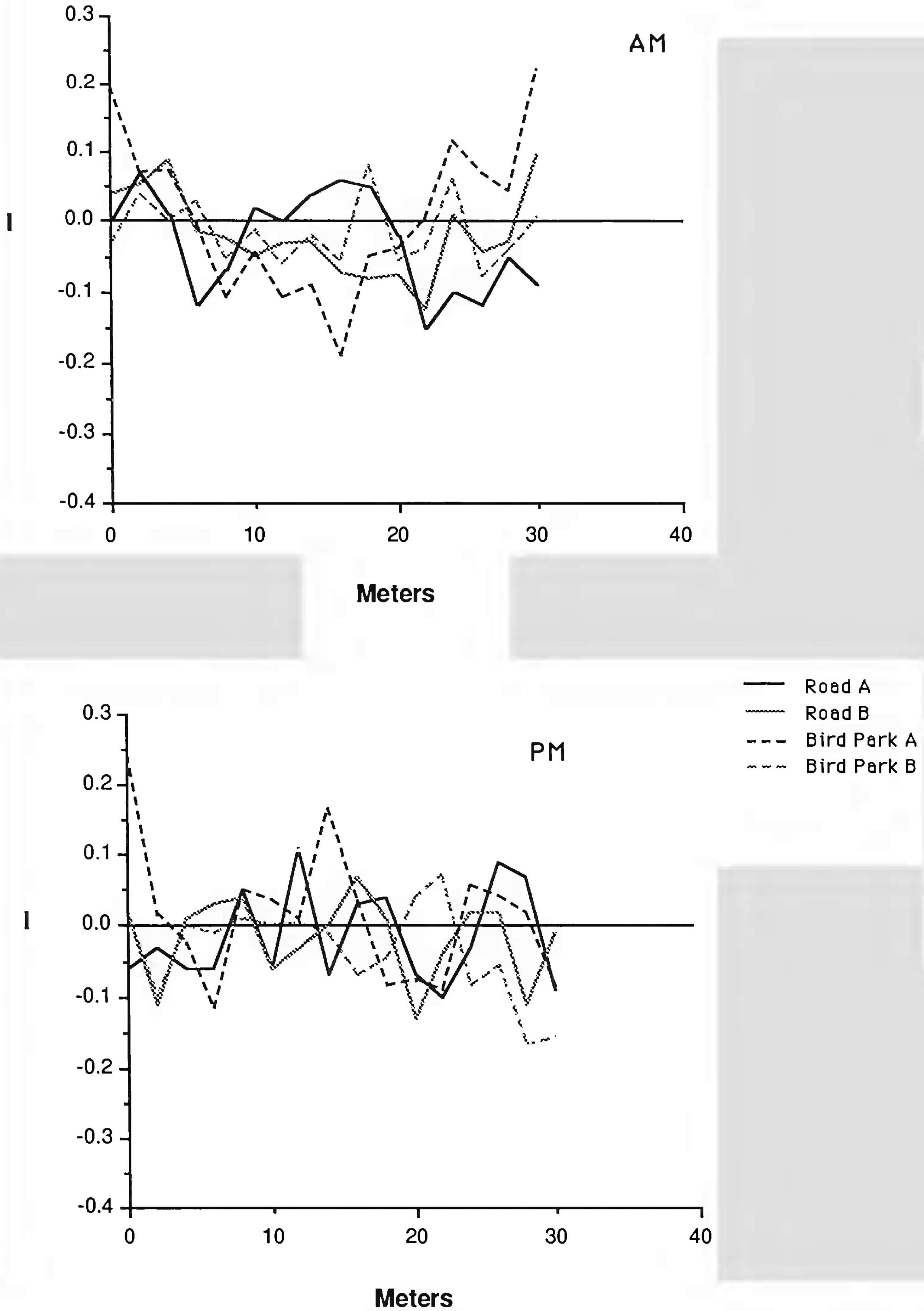

Figure 2. Correlogram for the number of *D. floricola* versus *D. floricola* adults per blossom as a function of distance (meters) between blossoms. The four lines represent the four sites. The upper and lower figures are for morning and evening censuses, respectively.

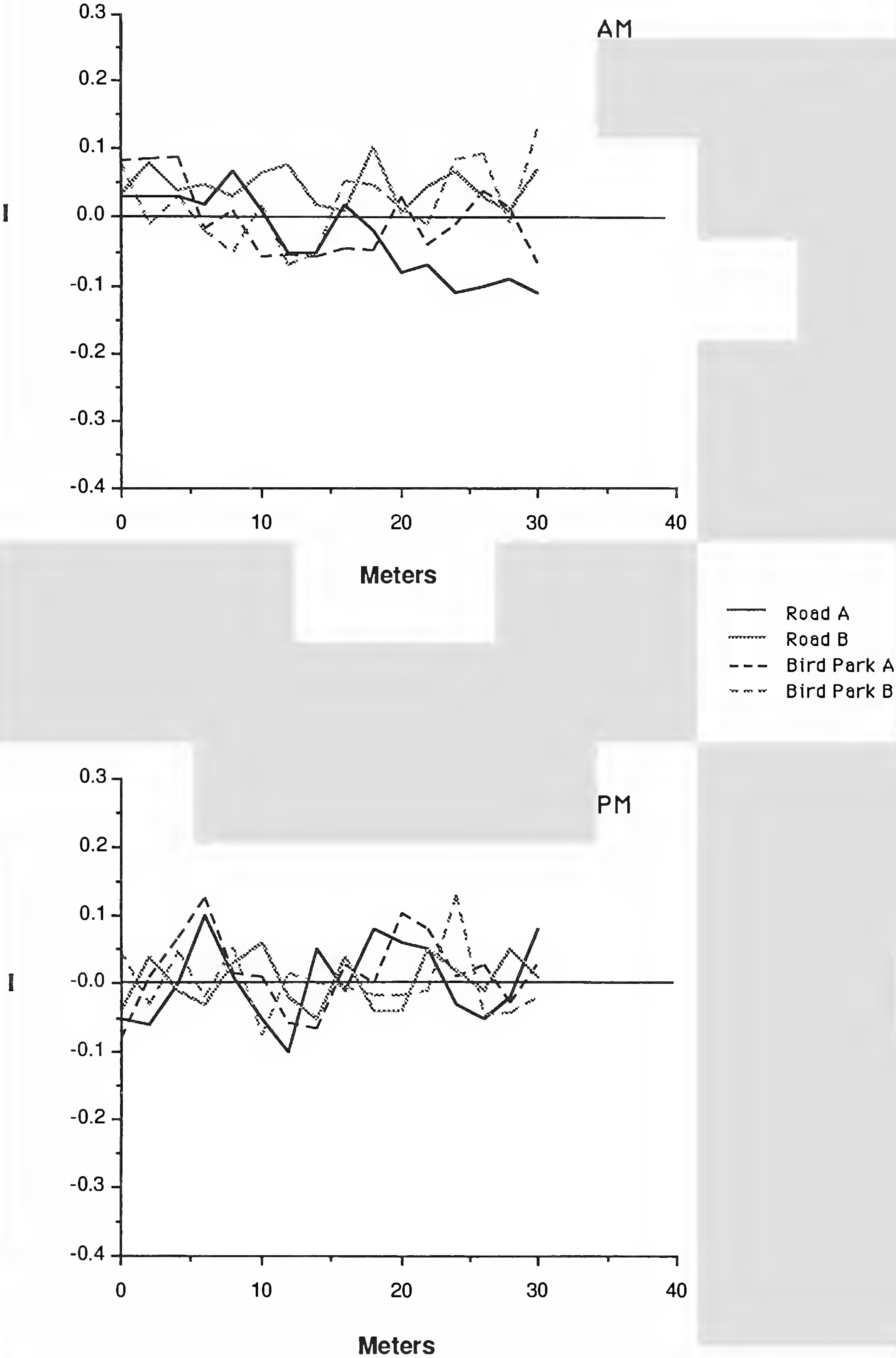

Figure 3. Correlogram for the number of *S. caliginosa* versus *D. floricola* adults per blossom as a function of distance (meters) between blossoms. The four lines represent the four sites. The upper and lower figures are for morning and evening censuses, respectively.

population cages at densities similar to that in the field and provided with fresh morning glory blossoms, adults of both species are reared from the same individual blossoms. This result in conjunction with the spatial structure of the two species we have documented in this report makes it likely that the opportunity for larval competition exists under field conditions. However, other factors such as the use of blossoms of other plant species as a refuge by the introduced species (Montague & Kaneshiro 1982) could influence coexistence of the two species (Shorrocks 1990). We are also aware of the possibility that because most of our observations are confined to one season over several years, we are missing important seasonal variation in the distribution of the two species. It is important to establish the status of these species over time and space during this relatively early stage of encounter in this unique habitat.

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